Migratory behaviour and survival rates of wild northern Atlantic salmon (*Salmo salar*) post-smolts: effects of environmental factors

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Running headline: Migration and survival of northern post-smolt

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ABSTRACT

To study smolt behaviour and survival of a northern Atlantic salmon (*Salmo salar*) population during river descent, sea entry and fjord migration, 120 wild *S. salar* were tagged with acoustic tags and registered at four automatic listening station arrays in the mouth of the North Norwegian River Alta and throughout the Alta Fjord. An estimated 75% of the post-smolts survived from the river mouth, through the estuary and the first 17 km of the fjord. Survival rates in the fjord varied with body length, and ranged from 97.0–99.5% per km. On average, the post-smolts spent 1.5 days (36 h, range 11–365 h) travelling from the river mouth to the last fjord array, 31 km from the river mouth. The migratory speed was slower (1.8 bl sec^{-1}) in the first 4 km after sea entry compared to the next 27 km (3.0 bl sec^{-1}). Post-smolts entered the fjord more often during the high or ebbing tide (70%). There was no clear diurnal migration pattern within the river and fjord, but most of the post-smolts entered the fjord at night (66%, 2000–0800 hours), despite the 24 h daylight at this latitude. The tidal cycle, wind-induced currents and the smolts' own movements seemed to influence migratory speeds and routes in different parts of the fjord. A large variation in migration patterns, both in river and fjord, might indicate that individuals in stochastic estuarine and marine environments are exposed to highly variable selection regimes resulting in different responses to environmental factors on both temporal and spatial scales. Post-smolts in northern Alta Fjord had similar early marine survival rates to those observed previously in southern fjords; however fjord residency in the north was shorter.

Key words: sea entry; diurnal migration; horizontal distribution; migratory speed; acoustic telemetry; Program MARK.

INTRODUCTION

Over the last decades, the abundances of many Atlantic salmon (*Salmo salar* L.) populations in Europe and North America have declined drastically (Hansen *et al.*, 2008; ICES, 2008). In contrast, most of the populations in northern Norway and Russia have not experienced the same reductions (Niemelä *et al.*, 2004). While reasons for the continued decline are not entirely clear (Parrish *et al.*, 1998), the period of sea entry and first phase of marine life is often considered to be the time at which the majority of marine mortality occurs (Jacobsen & Hansen, 2000; Hvidsten *et al.*, 2009).

In a recent study, Rikardsen *et al.* (2004) showed that post-smolts had higher feeding rates in the northern fjords more so than those from southern fjords along the Norwegian coast. Northern populations also had the largest and oldest smolts, potentially reducing the risk of predation while entering the sea. Later, Knudsen *et al.* (2005) used marine endoparasites as bio-indicators of feeding and sea residence of post-smolt and reported a prolonged feeding migration up to several weeks in northern fjords compared with those in the south. Overall, however, little information exists about the early marine survival and migration pattern in southern populations (Lacroix *et al.*, 2004b; Thorstad *et al.*, 2007; Lacroix, 2008) and virtually no published information exists on the early marine survival during sea entry and duration of migration of northern populations.

Among factors that can affect the migration behaviour and survival is the fjord morphology. Many southern Norwegian fjords are characterised by long and narrow sill fjords with several rivers draining into them, resulting in a brackish surface water layer. North Norwegian fjords are often shorter and wider with only one main river in the fjord bottom. They are usually more productive, more strongly influenced by the coastal and tidal current, and with less clearly defined sills (Rikardsen *et al.*, 2004). As potential predators are most abundant within fjords (Hvidsten & Lund, 1988; Svenning *et al.*, 2005), a long fjord may increase the predation risk. A longer fjord residency, as postulated for post-smolt in the northern fjords (see above), also increases predation risk.

The northernmost post-smolts are exposed to 24 h sunlight during their migration (Veselov *et al.*, 1998; Davidsen *et al.*, 2005), in contrast to the southern populations, for whom the sun sets at night. In the south, smolt migration usually takes place at night. However, towards the end of the migration period and during periods with high water temperatures, migration may take place both night and day (Hvidsten *et al.* 1995, Ibbotson *et al.* 2006). Nocturnal migration might be a strategy to prevent or minimize predation by visual predators (Solomon, 1982; Jepsen *et al.*, 2006), and this migration pattern seems to continue when smolts are entering the sea, as most smolts seem to enter salt water during hours of darkness (Moore *et al.*, 1995; Koed *et al.*, 2006). In contrast, the within-river smolt migration in northern rivers with 24 h light showed smolts descending during both night and day (Veselov *et al.*, 1998; Davidsen *et al.*, 2005). For northern populations, no information has been published on the timing of smolt migration into the fjord.

Overall, there is a lack of information on early ocean migrations, especially for northern *S. salar* populations. Given the potential importance of the initial life-history stage of post-smolts at sea to overall marine survival, the focus of this study was to examine the survival and migratory speeds of northern smolts and post-smolts during i) final within-river migration, ii) sea entry, and iii) fjord migration. The observed fish behaviour was correlated with the tidal cycle, day and night periods, fjord currents and wind speeds and directions.

MATERIAL AND METHODS

STUDY AREA

The River Alta, northern Norway (70°N 23°E), has a mean annual water discharge of 75 $m^3 s^{-1}$ and a catchment area of 7 400 km^2 (Fig. 1). A 46 km long river stretch is available to *S. salar*. The river drains into the Alta Fjord, which has three channels to the northern Atlantic. This is a large, open fjord, which is 15 km at its widest and 488 m at its deepest. Tidal range is about 1.5–2.5 m. The temperature in the river usually varies from 10–15° C during the main smolt run, which occurs during late June–middle July (Hvidsten *et al.*, 1998).

SMOLT CAPTURE AND TAGGING

A smolt trap (fyke net with guiding fences) operated 11 km upstream of the river mouth during the entire smolt run in 2004–2006 (22 June–17 July 2004, 17 June–27 July 2005 and 14 June–02 August 2006). In 2007, the trap was operating from 24 June–17 July, only covering the last half of the smolt run. The diurnal pattern of the smolt decent was therefore based on the 2004–2006 catches. The trap was emptied 2–4 times every 24 hours, with day catches sampled from 0700–1000 hours until 1800–2200 hours, and night catches sampled from 1800–2200 hours to 0700–1000 hours. Number of fish caught per hour was used as an indication of the movement of the smolt. Smolts were distinguished from parr based on external phenotypic characteristics (Wedemeyer *et al.*, 1980). Only 1% of smolts were smaller than 120 mm fork length (L_F).

In 2007, 120 wild smolts caught in the smolt trap were tagged with individually coded acoustic transmitters (Thelma AS, Norway, model LP-7.3, diameter of 7.3 mm, length of 18 mm, mass in water/air of 1.2/1.9 g). The smolts were tagged during two periods, 26–

28 June (period 1, n = 60, mean L_F 146 mm, range 133–168 mm, S.D. = 6; mean mass 28 g, range 22–39 g, S.D. = 4) and 2–4 July (period 2, n = 60, mean L_F 147 mm, range 134–177 mm, S.D. = 9, mean mass 30 g, range 22–51 g, S.D. = 6). There was no difference in body length (t-test, n = 120, P = 0.63) or mass (t-test, n = 120, P = 0.10) between the two groups. The smolts were kept in a tank with circulated water for up to two hours before tagging. Surgical implantation of transmitters was performed as described in Davidsen *et al.* (2008). Approximately ten minutes after recovery, the smolts were released into the river at the capture site. In each period, the smolts were tagged and released into four groups (n = 15 in each group), of which two groups were released at 0900–1000 hours and two at 2100–2200 hours.

RECORDING OF FISH BY AUTOMATIC LISTENING STATIONS AND MANUAL TRACKING

Two automatic listening stations (ALS) (Vemco INC, Canada, model VR2) were deployed two meters below the water surface in the river mouth (Fig. 1). Three ALS arrays were deployed across the fjord at 4 km (11 ALSs), 17 km (14 ALSs) and 31 km (21 ALSs) from the river mouth (Fig. 1). The ALSs within each array were deployed five meters below the water surface and separated horizontally by 400 m. The ALSs recorded the acoustic id code of the tagged post-smolts and the time from when they were within a range of 50–300 m from the ALS (detection range depended on environmental conditions). The last registration of individual smolt in the river mouth was used as the time of sea entry. At the three arrays in the fjord, the first registration was used as the time of arrival at the array. Manual river tracking was performed every second week during 28 June–14 October by using an acoustic receiver with an omnidirectional hydrophone (Vemco INC, Canada, model VR100) to detect any smolts remaining in the river.

ENVIRONMENTAL VARIABLES

Environmental variables (temperature, salinity, tidal cycle, light intensity, water current and wind speed and direction) were recorded in the fjord. Temperature and salinity were measured in order to describe the fjord system, while tidal cycle, light intensity, water current and wind speed and direction were correlated with post-smolt behaviour. Salinity and temperature profiles were recorded at every second ALS across all arrays down to 12 meters depth on 6 July at low tide (Fig. 2), using an SD204 CTD-sonde (SAIV AS, Norway). The dataset was analysed, gridded and plotted using Matlab7.0.4.365 (R14). The tidal cycle was recorded using a depth sensing data storage tag (Star-Oddi, Iceland, model DST-milli-L) placed at the fjord bottom 1 km from the river mouth, storing data every 10 minutes. An SD6000 water current meter (Sensordata AS, Norway) was placed three meters below the surface at the southern and northern side of the innermost array (Fig. 1), recording the direction and velocity of the water current every 30 min (Fig. 3). A light meter and a wind meter (anemometer) with a data logger (Onset Computer Corporation, USA, model HOBO UA-002-64) were placed on a small island in the inner part of the fjord (Fig. 1), recording light intensity, wind speed and wind direction every 15 minutes.

DATA ANALYSES

Not all post-smolts migrating through the fjord were registered at each ALS array. There are three reasons why fish might not be detected by a specific array. The post-smolts may have died at an earlier stage, they may have passed without being registered (not ‘captured’) or the acoustic tag failed. To solve the problem of confusion between the two first mentioned factors, the results were analysed as a capture-mark-recapture (CMR) experiment, where a registration on an ALS array was regarded as a recapture. CMR modelling provides maximum likelihood estimates of survival between the ALSs arrays and for the probability of registration by each array. An exception is for the last sampling interval (between the second and third array), where survival and registration are confounded. For this reason, survival can not be estimated between these two last arrays and probability of capture cannot be estimated for the last array.

Using the Program MARK (White & Burnham, 1999), 14 models of varying complexity were fitted for hypothesis testing (See Lebreton *et al.*, 1992 for more details). The global model [Surv(G*D), Recapt(G*D)] included interaction effects between survival rate (Surv), tagging groups (G), distance-dependency (D) and recapture rates (Recapt). Body length and mass were included as individual covariates. The other 13 models were all nested models from the global model. The hypothesis that the survival rate of post-smolts was size dependent and changed with distance moved from the release site was tested with a Cormack-Jolly-Seber (CJS) mark-recapture model for live recaptures. Probabilities of 'capture' (registration) at each ALS array and survival rates between the arrays were, in addition, estimated. To allow comparison of survival between the ALS arrays, survival estimates were scaled to the distance between arrays to provide an estimate of survival per km. Body length and mass at tagging were included as individual covariates. Three approaches for modeling the individual covariates were used: body size with no trend, a linear trend on body size, or a second order quadratic trend on body size.

The CJS model assumes that all individuals in a release group behave identically (that is, they have common survival and recapture probabilities), and that all survival and recapture probabilities are independent (Cormack, 1964; Jolly, 1965; Seber, 1965). Before conducting the analysis, a goodness-of-fit (GOF) test for each tagging group was performed using the program UCARE V2.2.5 (global test) (Choquet *et al.*, 2005) to determine whether the assumptions of the CJS model were violated. The GOF test indicated (first tagging group: *P*(Chi-square) = 0.91, df = 6; second tagging group: *P*(Chi-square) = 0.91, df = 6) that the global model described the data adequately, indicating that the assumptions of the CJS model were not violated. The approximating models were compared using Akaike´s Information Criterion (AIC) (Anderson *et al.*, 2001). AIC ranks the candidate models to determine which model provides the best description of the data with the fewest parameters.

Time spent in the different parts of the fjord system and migratory speeds could be calculated only for those post-smolts recorded both entering and leaving a particular fjord location. The sample sizes for these analyses were, therefore, smaller than the total number of post-smolts recorded. Migratory speed was estimated as individual body lengths per second and km per hour by using the shortest distance between the river mouth and the arrays, thus giving minimum estimates (Thorstad *et al.*, 2004; Økland *et al.*, 2006).

To test if post-smolts followed outgoing currents when passing the first ALS array, time of post-smolt passage at the two ALSs positioned nearest to each of the two current meters were compared to the current speed and direction. To test if smolt and post-smolts migrated during day or at night, night time was defined as 2000–0800 hours, corresponding to light intensities less than 20 000 lx.

Potential differences in survival between post-smolts entering the fjord during day or night and during the different phases in the tidal cycle (divided into three hour phases: high, ebbing, low or flooding tide) were tested by using registration (‘recapture’) rates from the river mouth and the second ALS array. Since the survival analysis in Program

MARK showed that the recapture rate was constant (see results), it could be assumed that timing of sea entry did not affect the registration rate by the ALS arrays. Following this, the registration rate in this case was the same as the survival rate, and a Chi-square test was used to test for differences in the proportion from each of the groups (i.e. day/night and tidal phases) that survived from the river mouth to the second array 17 km from the river mouth.

Differences in the horizontal distribution along the different ALS arrays were tested with Spearman's rank correlation and differences in the horizontal distribution between periods with and without wind were tested with a Chi-square test. To take into account the time lag of wind forces on the water currents, mean average wind speed and direction from the last four hours (corresponds to mean average time used for the last three km before the array) before the passage of the post-smolt in the ALS array were used. Due to the low number of post-smolts registered at each ALS array, the wind speeds were divided into two categories: "no wind" was defined as wind speeds less than 3.0 m sec^{-1} and "wind" as wind speeds from 3.1–12.5 m sec^{-1} (highest measured value).

RESULTS

In total, 98 (82%) of the 120 smolts were registered at least on one occasion following release. Of these, 86 (72%) were detected in the fjord while 12 (10%) were only registered during manual tracking in the river. The remaining 22 smolts (18%) were never registered after release. Sixty four post-smolts (53%) were registered in the river mouth, 46 (38%) by the first array, 46 (38%) by the second array and 34 (28%) by the third array.

The first detection in the river mouth was two days after release and the last detection 48 days after release. The groups of smolts released during the day or night did not differ in within-river survival (Chi-square test, first tagging group, *n* = 31, *P* = 0.37; second tagging group, *n* = 33, *P* = 0.60) or in the diurnal timing of sea entry (Chi-square test, first tagging group, *n* = 31, *P* = 0.70; second tagging group, *n* = 33, *P* = 0.51). The same was true for the groups of smolts released in late June and early July (Chi-square test, pooled groups, survival, *n* = 64, *P* = 0.80; diurnal timing of sea entry, *n* = 64, *P* = 0.95). These groups were therefore pooled in the following analyses.

SURVIVAL RATES

Overall, 75% (95% CL: 63–89%) of the post-smolts were estimated to survive during the first 17 km of the fjord migration. The survival rate in the fjord depended on fish body length (Table I). For post-smolts at 140 mm body length, the survival rate was estimated at 99.5% per km and for post-smolts at 150 mm length 97.0% per km (Fig. 4). This means that the model estimates that 92% of the 140 mm and 60% of the 150 mm post-smolts survived to the second ALS array 17 km from the river mouth. The survival rate in the river increased with body length and ranged from 97.5–99% per km (Fig. 4). The best approximating model indicated that there was no difference in survival between the first (river mouth to first array) and second fjord zone (first to second array) (Table I). There was also no difference in survival between individuals from the two tagging periods (period 1 and 2) or as a function of individual mass (Table I), and the registration rates at the ALS arrays (‘recapture rates’) were not a function of any of the components included in the model.

MIGRATORY SPEED

The smolts spent from 7–1309 h (mean = 113 h, S.D. = 222) migrating the 11 km downstream the river from the release site to the river mouth. Mean migratory speed was 0.3 km h^{-1} (range 0.0–1.6 km h^{-1}) corresponding 0.5 bl sec^{-1} (Table II). Time spent from the river mouth to the last array 31 km along the fjord varied from 11–165 h (mean = 36 h, S.D. = 32). The migratory speed was slower from the river mouth to the first array (1.0 km h^{-1}; 1.8 bl sec^{-1}) than from the first to the second array (1.6 km h^{-1}; 3.0 bl sec^{-1}) (*t*-test (bl sec^{-1}), *n* = 59, *P* = 0.005). There was no difference in migratory speed from the first to the second, and from the second to the third array (1.7 km h^{-1}; 3.1 bl sec^{-1}) (*t*-test (bl sec^{-1}), *n* = 48, *P* = 0.90) (Table II).

EFFECTS OF ENVIRONMENTAL FACTORS ON THE MIGRATION PATTERNS

Salinity and temperature varied with location, depth (Fig. 2) and time, but salinity generally increased along the fjord. Forty three (70%) of the 62 post-smolts that were registered in the river mouth before the termination of the environmental measurements entered the sea during high tide (24, 39%) or ebbing tide (19, 31%) (Table III). More post-smolts passed the north-eastern current meter of the first ALS array on ingoing currents (14) than on outgoing currents (4) (Chi-square test, *n* = 18, *P* < 0.001) (Fig. 3). No such difference was found at the south-western current meter (Chi-square test, *n* = 8, *P* = 0.42) (Fig. 3). The current speeds (< 15 cm s^{-1}, Fig. 3) were all the time well below the estimated migratory speed of post-smolts between the river mouth and first ALS array (27 cm s^{-1}, Table II). The current measurements showed that the variation of current direction could not be explained by the tides alone. At the north-eastern current meter, the tide modulated (accelerated and retarded) the current speed, but the current direction did not change with every tidal period (Fig. 3). The measurements from the south-western current meter showed less regular variation. The dominating current directions were into and out of the fjord at both current meter locations. The currents at the two current meters did not co-vary. The currents at the two locations were flowing in opposite direction on several occasions, indicating episodes with both clockwise and counter-clockwise circulation in the fjord. However, periods with currents flowing in the same direction at the two current meters were also recorded.

There was a clear difference in the light intensities between day (20 000–209 424 lx) and night (54–20 000 lx) during the study period (26 June–18 July). There was no difference in the number of smolts caught day or night in the trap in the river (Table IV). Similarly, there was no difference between day and night in the time of arrival of tagged post-smolts at the three ALS arrays in the fjord (Table V). However, more smolts entered the fjord from the river by night (Chi-square test, $n = 39$, $P = 0.01$) (Table III). When combining tidal water and time of the day, 31 (50%) of the smolts left the river mouth at high (17, 27%) or ebbing tide (14, 23%) during the night (Table III). A larger proportion of the post-smolts that entered the sea during day (71%) than at night (59%) survived to the second array (Table III). Similarly, a larger proportion of the post-smolts that entered the sea at low tide (91%) than at high tide (67%) survived the same distance. The largest proportion of survivors came from the groups of post-smolts that entered the sea at low (100%) and high (86%) tide during day time and at low tide during night time (86%) (Table III).

There was a tendency for the post-smolts to migrate on the north-eastern side of the fjord when passing the innermost array (Spearman's rank correlation, $n = 46$, $P = 0.08$). However, when passing the second ($n = 46$, $P = 0.03$) and third array ($n = 34$, $P < 0.001$), the horizontal use of the fjord increased towards the western side of the fjord. The horizontal distribution at the second array differed between periods with and without wind. During periods with no wind (wind speeds < 3.0 m sec^{-1}), the post-smolts were evenly distributed across the ALS array (Chi-square test, $n = 21$, $P = 0.87$), while when the wind was blowing (wind speeds: 3.0–12.5 m sec^{-1}) from the east (wind direction: 51–140°), almost all post-smolt passed the array on the western side of the fjord ($n = 10$, $P < 0.001$) (Table VI). There was no difference between periods with and without wind in the horizontal distribution when the post-smolts passed the first and third ALS array.

DISCUSSION

SURVIVAL RATES

The estimated post-smolt survival rate of 75% over the first 17 km through the estuary and fjord indicates that post-smolts in the northern Alta Fjord had a relatively high mortality during the first days after sea entry. This is particularly clear when taking into consideration that the study covers only a small fraction of their 1-3 year marine period of the potentially lengthy migration through the northern Atlantic and Barents Sea (Holst *et al*., 2000; Rikardsen *et al*., 2008). Therefore, these results provide further support for the general belief that the period of first migration to sea is critical in the overall survival of salmon at sea.

The transition from freshwater in the river to saline water in the estuary and fjord may be a critical period for the post-smolt. Osmotic stress is suggested to involve a less effective antipredator behaviour (Handeland *et al.*, 1996) and the exposure to predators immediately after sea entry is high (Hvidsten & Lund, 1988; Dieperink *et al.*, 2002). The observed survival rates were higher in the north than those observed in Romsdalsfjorden, southern Norway, where 35% of similarly tagged wild post-smolts survived the first 37 km from the river mouth (Thorstad *et al.*, 2007), but lower than in Passamaquoddy Bay in

Canada where 82% of 38 wild post-smolts survived the first 20 km of migration through the bay (Lacroix *et al.*, 2004b). However, the mean L_F of the Passamaquoddy Bay post-smolts was 187 mm, while the mean L_F of post-smolts in Romsdalsfjorden and this study were only 152 and 147 mm, respectively. Negative size selective mortality has been observed in several studies (Eriksson, 1994; Thorstad *et al*., 2007), and the differences in body length may be one explanation for the higher survival rate found by Lacroix *et al.* (2004b).

Smaller smolts had the lowest survival rate in the river, but not in the fjord. This may be due to a combination of increased predation rate and possible tagging effects, since smaller smolts may be more vulnerable to the surgical implantation (Jepsen *et al.*, 2002; Lacroix *et al.*, 2004a). The smolts were tagged and released 11 km upstream the river, and were therefore expected to be recovered from tagging stress at the time of sea entry. If survivors from the smallest size group in the river represent the best adapted smolts, this may explain why the size selective mortality was observed only in the river and not in the fjord, as opposed to in the studies of Eriksson (1994) and Thorstad *et al.* (2007). Tagged smolts in those studies were released in the river mouth and a size selective mortality occurred in the fjord. Twenty-two (18%) of the smolts in the present study were never registered after release, which may be due to predatory birds bringing the smolts out of the river, malfunctioning transmitters, or the smolts moving or drifting to a place where the detection efficiency was low (like rapids and other places with high current speeds). The present study demonstrates that northern post-smolts also seem to have a relatively high mortality during migration through the estuary and fjord.

MIGRATORY SPEED

The migratory speed out of the fjord (mean 1.5 days during the first 31 km) was slightly higher than in studies from more southern areas. Wild post-smolts in the south Norwegian Romsdalsfjorden spent on average 5.6 days passing the first 48 km of the marine migration (Thorstad *et al.*, 2007), and in the Passamaquoddy Bay in North America, post-smolts migrated the first 23–36 km through the bay in 2–6 days (Lacroix & McCurdy, 1996; Lacroix *et al.*, 2004b). The results are, therefore, contrary to the expectations based on both the earlier hypothesis of potential prolonged fjord residency of northern post-smolts due to generally better feeding conditions in the north (Rikardsen *et al*., 2004), and the results of Knudsen *et al.* (2005), who found that the high intensity of trophically transmitted parasites in some of the northern post-smolts supported this theory. As there is no information available on the feeding intensity of the fish in the present study, it was not possible to verify if the fjord feeding affected their migratory speed. It might be that the years studied by Knudsen *et al.* (2005) had a higher food abundance and that some smolts prolonged their fjord feeding period due to this. However, feeding in the Alta Fjord seem anyhow to be generally more extensive and less variable between years than observed in the southern Norwegian fjords (Rikardsen *et al*., 2004; Hvidsten *et al*., 2009). Therfore, an assumed high initial feeding rate combined with the observed fast seaward migration, may result in a reduced chance of being eaten by predators and a high immediate growth rate for the survivors, thus contributing to a potentially better start to the marine life for the post-smolt in the northern Alta Fjord compared to the generally much longer and less productive southern Norwegian fjords.

There was a large individual variation in migratory speeds, which may indicate that the individuals encountered different current speeds and directions at sea entry. Alternatively, this may be an indication of individual behaviour. The fact that the mean migratory speed was always higher than the measured current velocities indicates that the post-smolts had an active swimming behaviour, which is consistent with other observations (Thorstad *et al.*, 2004; Økland *et al.*, 2006). Despite the individual variation, post-smolts spent a significantly longer time in the inner part of the fjord than in the more saline outer parts. Hoar (1988) found that post-smolts may not need a period of acclimatisation in the estuary because they have previously, while still in fresh water, become modified physiologically to tolerate saline conditions. However, another reason for the lower migratory speed in the estuary may be due to the complexity of the Alta Fjord system, which could make orientation to open waters more difficult for the post-smolts. Since the smolts were captured, tagged and released in the river and on average spent two to four days in the river before sea entry, short term effects from tagging and handling were not expected to be the causes for the initial low migratory speed in the fjord. The findings of an increased migratory speed out of the fjord are in accordance with observations at Gaspé Bay, Canada, where it was found that exposure to more saline waters caused increased swimming speeds, and migratory speeds were higher in the outer and more saline part of an embayment (Hedger *et al.*, 2008). These findings are also consistent with observations from Romsdalsfjorden, southern Norway (Finstad *et al.*, 2005; Thorstad *et al.*, 2007) and from the River Conway, Wales (Moore *et al.*, 1995). Thus, post-smolts seem to increase their fjord migratory speed the more familiar they become with their habitat and the closer they get to the open ocean.

EFFECTS OF ENVIRONMENTAL FACTORS ON THE MIGRATION PATTERNS

A majority (70%) of the post-smolts entered the sea at high or ebbing tide. Swimming in outgoing tide currents speeds up the migration during the first hours through the estuary. Since predation on salmonid post-smolts in the river mouth and estuary can be a major mortality factor (Hvidsten & Lund, 1988; Jepsen *et al.*, 2006), a fast migration through these areas may reduce the predation risk.

However, the post-smolts did not seem to continue following an outgoing tidal current at the time they passed the first ALS array four km from the river mouth, since more post-smolts passed the array on ingoing currents. The complex current system in the inner part of the Alta Fjord may complicate the post-smolts outward migration, so they only were able to take advantage of an outgoing tidal current during a short period after sea entry. It may, therefore, be that the reason for the observed higher survival rate of post-smolts entering the sea at low tide (91%) than at high tide (67%) was that post-smolts entering the sea at high tide in this case had no, or only an initial, advantage by doing so. The findings are opposite to observations from Penobscot River estuary, where hatchery-reared *S. salar* post-smolts were found to passively drift on tidal currents (McCleave, 1978). However, this estuary is influenced by strong tidal currents with surface currents exceeding 200 cm s^{-1}, which is about ten times higher than observed in the River Alta estuary. The current meters used in the Alta Fjord were placed three meters below the water surface, in the halocline. If the post-smolts followed the brackish water layer closer to the surface, they may have experienced different current speed and directions than measured. However, Davidsen *et al.* (2008) found that post-smolts during the early seaward migration migrated at 1-3 meters depth, which corresponds to the depth of the current meters. To fully understand the fjord water mass dynamics and the effects on the post-smolt migration, current measurements are recommended to be taken at additional locations and depths within a fjord.

A larger proportion of the post-smolts entered the sea during night than during day. Nocturnal migration in temperate areas with dark nights is thought to be an adaptive behaviour to avoid or minimize predation by visual predators (Solomon, 1982). Even though the northern River Alta is situated on a latitude with midnight sun, light intensities were still lower than 20 000 lx at night, in contrast to the 50 000–200 000 lx measured during day time. The nocturnal migration pattern at sea entry may also be an anti-predator strategy in northern areas. When combining timing of sea entry with both time of the day and the tidal cycle, it was found that post-smolts entering the sea at high tide during day and low tide during night had a similar survival rate (86%). Despite small sampling groups, the findings indicate that the optimal strategy for timing the sea entry is far more complex than only timing to tidal cycles and day light. This is supported by observations from a study in the Usk Estuary, Wales, where the entrapment of smolts in the river mouth showed that the largest numbers of *S. salar* smolts were caught during the day on the flood tide and the least on an ebbing night tide (Aprahamian & Jones, 1997). However, both Moore *et al.* (1995) and Lacroix *et al.* (2004b) found that smolts mainly left the river during the night on ebbing tides. Thus, these observations may indicate that the optimal timing of sea entry may vary with different environmental conditions of the estuaries and with different impacts of predators.

A diurnal variation in the timing of migration was not observed in the catches in the smolt trap in the river, nor in the time of arrival at the three ALS arrays in the fjord. Daytime migration in northern rivers has been previously reported (Veselov *et al.*, 1998; Davidsen *et al.*, 2005), but this is first time it has been demonstrated in a northern fjord. The fact that the proportion of post-smolts entering the sea was larger at night than during the day, while there was no diurnal variation in the migration in the river and fjord, may be an adaptation to the increased predation risk immediately after sea entry (Hvidsten & Lund, 1988; Jepsen *et al.*, 2006). The pattern of smolt migration both day and night in northern rivers has been suggested to be a trade off between utilizing the warmer water in the day and the darker hours in the night (Davidsen *et al.*, 2005).

The significant relationship between wind direction and horizontal distribution of the post-smolts in the second ALS array shows that the migration routes in this part of the fjord were influenced by the wind-induced surface currents. The relationship between horizontal distribution and wind speed and direction found in the second ALS array, but not in the first or third, can be explained by the relevant fetch length being longer in the broad and open part of the fjord, where the second ALS array was positioned.

In conclusion, as with southern populations of *S. salar*, this study shows that the start of the marine migration of the northern post-smolts may be a bottleneck where they experience low survival rates compared to the rest of their marine phase. The migratory speed was high in the Alta Fjord compared with southern populations, and more smolts entered the sea at night at high or ebbing tide, which may be a strategy to reduce the predatory risk. The high migratory speed in combination with earlier observations of a higher immediate fjord feeding rate of northern compared to southern post-smolts, may indicate that they have a potentially better start to the oceanic feeding migration than their southern conspecifics. In years with an earlier or later migration period than observed in this study, survival rates and migratory behaviour may differ due to differences in temperature regimes and other environmental factors. However, the high variance in migration patterns, both in river and fjord, might indicate that individuals in stochastic estuarine and marine environments are exposed to highly variable selection regimes resulting in different responses to environmental factors on both temporal and spatial scales.

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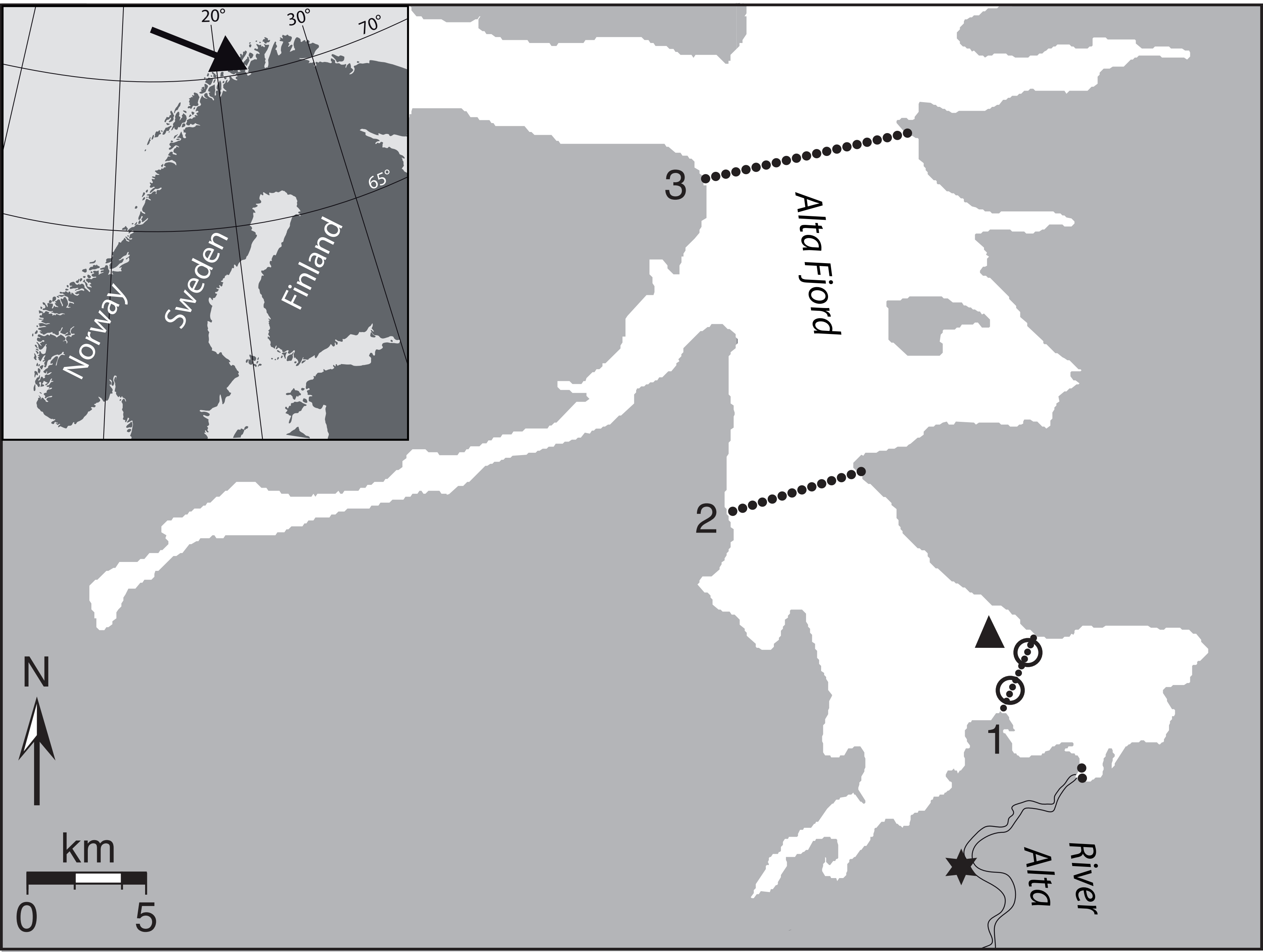
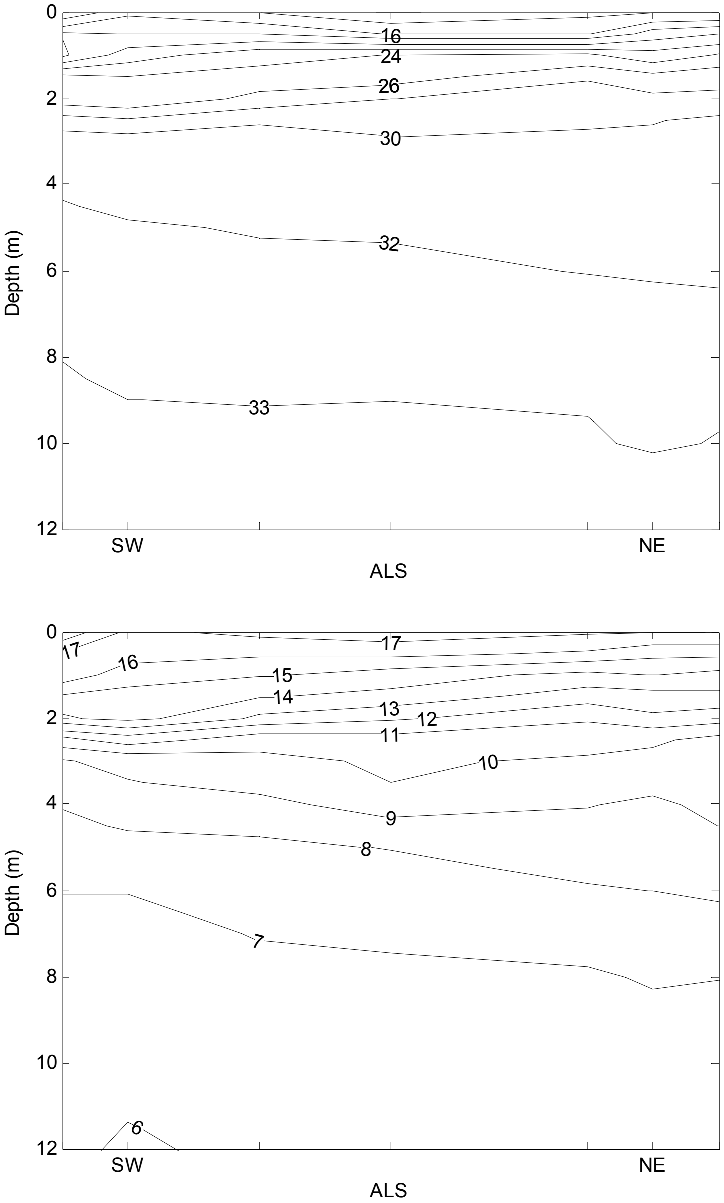
Figure


20°
30°
70°
65°
Norway
Sweden
Finland
3
Alta Fjord
2
1
River Alta
N
km
0
5

Figure


0
2
4
6
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10
12
Depth (m)
16
24
26
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SW
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Depth (m)
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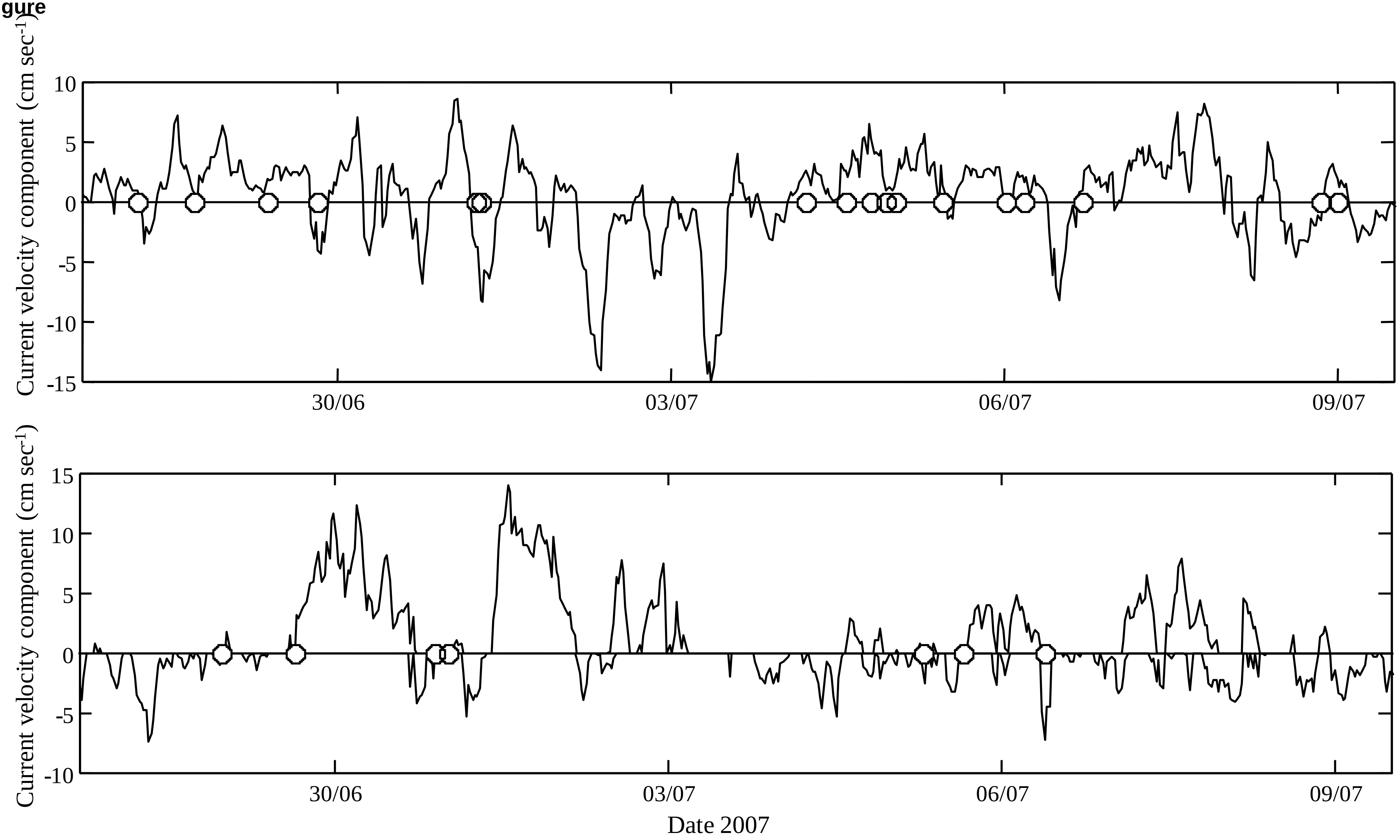
SW
NE
ALS

Figure


Current velocity component (cm sec-1)
10
5
0
-5
-10
-15
30/06
03/07
06/07
09/07
Current velocity component (cm sec-1)
15
10
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0
-5
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30/06
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09/07
Date 2007

Figure

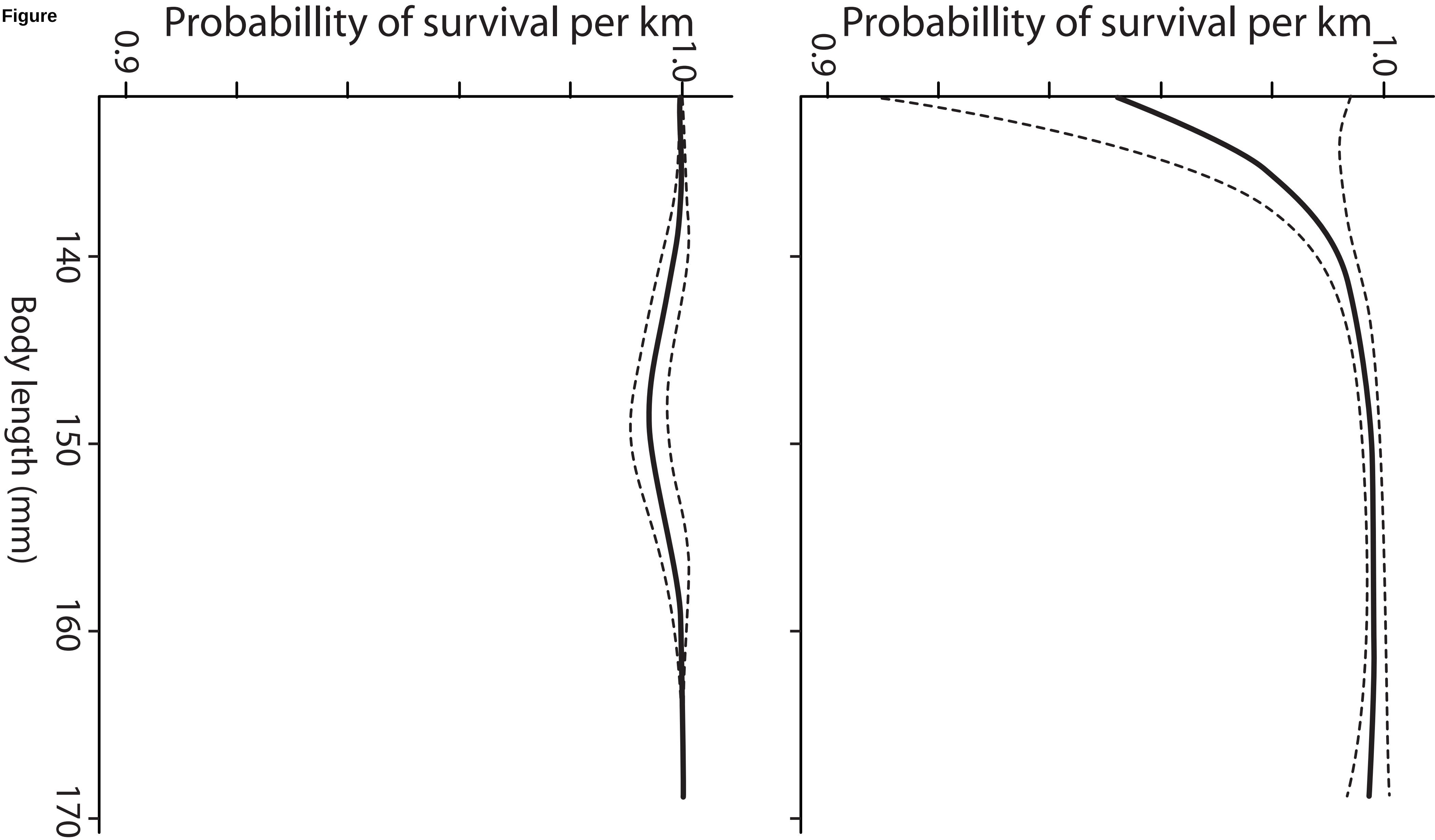
Probabillity of survival per km
0.9
1.0
Body length (mm)
140
150
160
170
Probabillity of survival per km
0.9
1.0

FIG. 1. Map of the lower part of River Alta and the Alta Fjord showing the release site (★), the two ALSs in the river mouth (•), the three ALS arrays in the fjord (•••••), the two current meters in the first ALS array (○) and the weather station (▲).

FIG. 2. Salinity (upper panel) and temperature (° C) (lower panel) distribution recorded at 0–12 m depth across the first ALS array in the Alta Fjord on 6 July 2007.

FIG. 3. Water current velocity at 3 m depth at the north-eastern (upper panel) and south-western (lower panel) side of the Alta Fjord at the first ALS array. The current velocity components were computed for the dominating current directions. Positive values are the velocity components towards the fjord head and negative values are towards the fjord mouth. ○ indicates time at post-smolt passage.

FIG. 4. *S. salar* smolt survival rates in the lower part of the River Alta (upper panel) and post-smolt survival rates in the Alta Fjord (lower panel) as a function of body length. Dotted lines show 95% confidence intervals.

TABLE I. Model selection for estimating survival of acoustically tagged *S. salar* post-smolts through the Alta Fjord. The table shows all 14 tested models. The models estimate survival (Surv) and recapture rates (Recapt) and include tagging groups (G), distance dependency (D), effects of the river and the fjord including three different fjord zones and the individual length and mass of the post-smolts. AICc is the score based on Akaike´s information criterium adjusted for small sample bias.

Model	AICc	Delta AICc	AICc weights	Model Likelihood	Number of parameters	Deviance
[Surv(.*D)Recapt(.*.)River effect, no fjord zone effect, indv. length quadratic std.]	574.32	0	0.88232	1	7	559.90
[Surv(.*D)Recapt(.*.)River effect, no fjord zone effect, indv. length]	579.86	5.54	0.05517	0.0625	5	569.64
[Surv(.*D)Recapt(.*.)River effect, no fjord zone effect, indv. length linear std.]	579.86	5.54	0.05517	0.0625	5	569.64
[Surv(.*D)Recapt(.*.)River effect, fjord zones, indiv. length]	584.88	10.56	0.00449	0.0051	9	566.20
[Surv(.*)Recapt(.*.)River effect]	588.02	13.71	0.00093	0.0011	2	583.98
[Surv(.*D)Recapt(.*.)River effect]	588.69	14.37	0.00067	0.0008	3	582.60
[Surv(.*D)Recapt(.*.)indiv. length]	589.49	15.18	0.00045	0.0005	6	577.18
[Surv(.*D)Recapt(.*.)]	589.64	15.33	0.00041	0.0005	5	579.42
[Surv(.*D)Recapt(.*.)indiv. mass]	591.27	16.96	0.00018	0.0002	6	578.96
[Surv(.*D)Recapt(.*D)]	591.30	16.98	0.00018	0.0002	7	576.88
[Surv(G*D)Recapt(.*)]	595.41	21.10	0.00002	0	9	576.74
[Surv(G*D)Recapt(.*D)]	597.19	22.88	0.00001	0	11	574.19
[Surv(G*D)Recapt(G*D)indiv. length]	599.25	24.93	0	0	16	565.15
[Surv(G*D)Recapt(G*D)]	603.23	28.92	0	0	14	573.62

TABLE II. Migratory speeds of acoustically tagged *S. salar* smolts in the River Alta and different parts of the Alta Fjord.

Receiver site	Distance (km)	Number of smolts recorded	Mean ± S.D. time (h) (range)	Mean ± S.D. migratory speed	
				($km\ h^{-1}$) (range)	($bl\ s^{-1}$) (range)
Release site–River mouth	11	64	113.0 ± 222.4	0.3 ± 0.3	0.5 ± 0.5
			(6.7–1308.7)	(0.0–1.6)	(0.0–3.2)
River mouth–array 1	4	33	5.8 ± 4.2	1.0 ± 0.5	1.8 ± 1.0
			(1.6–19.8)	(0.2–2.5)	(0.4–4.2)
Array 1–array 2	13	26	12.5 ± 9.2	1.6 ± 1.0	3.0 ± 2.0
			(3.2–36.4)	(0.4–4.1)	(0.7–7.3)
Array 2–array 3	14	22	11.9 ± 9.0	1.7 ± 0.8	3.1 ± 1.6
			(4.0–38.7)	(0.4–3.5)	(0.6–6.7)

TABLE III. Comparisons of the number and proportions of *S. salar* post-smolts entering the sea during 1) day and night, 2) at different stages of the tidal cycle, and 3) for different combinations of day and night and different stages of the tidal cycle. The number and proportions of post-smolts from each group surviving from the river mouth to the second array 17 km outward the fjord are also given, and differences in proportions of survivors among groups are compared with Chi-square tests and the *P*-value are given. * indicate groups having the significantly highest proportion of "time at sea entry". ** indicate groups having the significantly highest proportion of "survivors to the second array".

	Timing of sea entry			Survival from the river mouth to the second array in the fjord		
	Number of fish (*n* = 62)	%	*P*-value	Number of fish (*n* = 39)	%	*P*-value
Day time	21	34		15	71**	
Night time	41*	66	0.01	24	59	0.003
High tide	24*	39		16	67	
Ebbing tide	19	31		10	53	
Low tide	11	18		10	91**	
Flooding tide	8	13	0.02	3	38	< 0.001
High tide day time	7	11		6	86	
High tide night time	17*	27		10	59	
Ebbing tide day time	5	8		2	40	
Ebbing tide night time	14	23		8	57	
Low tide day time	4	6		4	100**	
Low tide night time	7	11		6	86	
Flooding tide day time	5	8		3	60	
Flooding tide night time	3	5	0.002	0	0	< 0.001

TABLE IV. Catch per hour (CPH) of *S. salar* smolts during day (0800–2000 hours) and night (2000–0800 hours) in a smolt trap operated in the River Alta during 2004–2006. *t*-tests were used to test for significant differences between day and night.

Year	Day (CPH)	Night (CPH)	Number of days of trapping	*P*-value
2004	5.1	7.1	25	0.53
2005	5.1	5	22	0.97
2006	1.4	1.7	19	0.61

TABLE V. Number and proportion of *S. salar* post-smolts arriving at each of the three ALS arrays in the Alta Fjord at day (0800–2000 hours) and night (2000–0800 hours). Chi-square tests were used to test for significant differences between the proportions.

Time of the day	Array 1	Array 2	Array 3
Day	21 (41%)	26 (49%)	20 (56%)
Night	30 (59%)	27 (51%)	16 (44%)
P-value	0.21	0.89	0.51

TABLE VI. Numbers of *S. salar* post-smolts registered at the western, central or eastern side of the ALS arrays in the Alta Fjord at different wind directions. Chi-square tests were used to test for significant differences in the horizontal distribution between periods with and without wind (wind speeds < 3.0 m sec^{-1}). * indicates if a part of the fjord had a significantly different high proportion of post-smolts registered during a certain wind direction.

	Wind directions (Degrees)	Side of the fjord (Number of post-smolts)			*P*-value
First array		South-west	Central	North-east	
	No wind	6	6	13	
	51–140	3	2	3	0.63
	141–230	0	1	5	0.26
	231–320	0	0	0	
	321–50	2	4	1	0.075
Second array		West	Central	East	
	No wind	7	6	8	
	51–140	9*	0	1	< 0.001
	141–230	5	4	2	0.39
	231–320	0	0	0	
	321–50	1	0	3	0.27
Third array		West	Central	East	
	No wind	7	4	4	
	51–140	6	4	1	0.41
	141–230	4	1	0	0.27
	231–320	0	0	0	

321–50	3	0	0	0.18